MYRMECOPHILY IN THE EDWARD'S HAIRSTREAK BUTTERFLY *SATYRIUM EDWARDSII* (LYCAENIDAE)

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ABSTRACT. Observations on the life history and myrmecophilous relationship of the lycaenid butterfly, *Satyrium edwardsii* (Grote and Robinson) and the ant, *Formica integra* Nylander, are described. *S. edwardsii* departs from other North American Lycaenidae in that the 3rd and 4th instar larvae aggregate during the day (in groups of up to 114 individuals per host) at the base of the host plant (*Quercus velutina* and *Q. coccinea* saplings) within conical structures of detritus (byres) constructed by the ants. The larvae leave the byres at dusk, feed nocturnally, and are usually surrounded by a group of attending ants. A membracid, *Similia camelus* (Fabricius), was abundant on the same host plants and was ant attended. We suggest that membracids associated with *S. edwardsii* larvae may be involved in the symbiotic relationship between *S. edwardsii* and *F. integra*.

Many species of Lycaenidae in North America are myrmecophilous (Downey, 1961, 1962; Harvey, 1980). The larvae are commonly surrounded by a group of ants that groom and palpate them with their antennae. On the 7th abdominal segment of late instar larvae is a dorsal gland, called Newcomer's organ, that secretes honeydew on which the ants feed (Newcomer, 1911; Malicky, 1970; Maschwitz et al., 1975). In addition, there are epidermal glands which secrete substances that attract and appease the ants (Malicky, 1970). In *Glaucopsyche lygdamus* (Doubleday) these attractive substances secure ant defense against parasitoid attack. This protection probably acts as a potent selective force in maintaining the symbiosis between lycaenid larvae and ants (Pierce & Mead, 1981).

The symbiotic relationship between ants and lycaenid larvae has received comparatively little attention for North American species, and in only a few cases have the associated ants been identified. Clark (1932) mentioned an association of *Satyrium edwardsii* (Grote & Robinson) with ants. Later Comstock (1940) reported that the eggs overwinter and that the larvae could be found in "ant nests" at the roots of scrub and scarlet oaks. Other than a brief larval description by Scudder (1889), little additional information is available on the biology of *S. edwardsii*. We here report on some observations of the life history and myrmecophilous relationship of *S. edwardsii* and the ant, *Formica integra* Nylander, in Michigan. It is our hope that this preliminary and somewhat anecdotal account will stimulate further studies on the myrmecophilous relationships between lycaenids and ants.

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STUDY AREAS AND METHODS

S. edwardsii has been reported from several localities in the lower peninsula of Michigan (Moore, 1960). We found this hairstreak to be abundant in the Flat River State Game Area, Montcalm Co., T9N, R7W, Sections 29–30 (Locality 1), and in Newaygo Co., T12N, R12W, Sections 1–2 (Locality 2). In these localities the primary host plants of *S. edwardsii* were black oak, *Quercus velutina* Lam. and scarlet oak, *Q. coccinea* Muench. A few larvae were also found on a *Q. alba* L. sapling in locality 2. Populations of *S. edwardsii* appeared to be closely associated with colonies of *F. integra*. Adjacent localities without *F. integra* did not support populations of *S. edwardsii* even though suitable host plants were present. Most of our observations were made at locality 1 in Montcalm Co. at various intervals (usually once a week) from April through July during 1980 and 1981.

Locality 1. The study area was a second growth woodlot of *Q. velutina*, *Q. coccinea* and *Q. alba* with a mixture of *Populus tremuloides* Michx., *Pinus strobus* L., and miscellaneus upland hardwood. *S. edwardsii* adults were abundant during July and occurred most frequently within a narrow, irregularly shaped opening of approximately 0.6 hectare. Within the opening were small *Q. velutina* and *Q. coccinea* with base diameters between 1.3 and 10.0 cm (most between 2.5 and 5.0 cm). Additional plants in the openings were *Lupinus perennis* L., *Ceanothus americanus* L., *Rudbeckia hirta* L. and assorted grasses and forbs. *C. americanus* appeared to be the major nectar source for the adults. The soil consists of Graying Sand (Schneider, 1960), a deep sand with low waterholding capacity. Five large (0.3–1.2 m dia.) nests of *F. integra* were in the opening.

Locality 2. This colony was located at the edge of a relict prairie. The same species composition of trees was found as at locality 1. *Q. velutina* saplings were the dominant species within the openings scattered within the second growth forest. Few other plants occurred in the openings other than grasses, forbs, and scattered clumps of *C. americanus*. The *F. integra* nests were smaller (no well defined mounds) and were situated within clearings. The soil was a Grayling Sand.

OBSERVATIONS

Larval, ant, and membracid associations. The eggs of *S. edwardsii* hatched during late April and early May when the oak buds were enlarged and ready to open. The reddish brown 1st instar larvae bored into the buds of *Q. velutina* and *Q. coccinea* saplings and suckers and fed diurnally. The 2nd instar larvae continued to feed on the buds and developing leaves. Buds with 1st or 2nd instar larvae usually had 2–4

larvae, but sometimes 6 or 7 were present. The larvae were frequently near nymphal aggregations of the membracid, *Similia camelus* (Fabricius) and scale insects (Coccoidea). These Homoptera release honeydew and were ant attended. The ants, in turn, defended any oak sapling having these Homoptera. When a sapling or branch was disturbed most ants assumed a defensive posture (reared up on pro- and mesothoracic legs with mandibles open, and sometimes pointed the abdomen anteriorly between the metathoracic legs), frequently moving toward the source of the disturbance. The ants readily attempted to bite any object brought near them. Although the 1st and 2nd instar larvae presumably can not produce honeydew (they do not have Newcomer's organs), ants were usually within 2.5 cm of each larva and appeared to tend them. We found Newcomer's organs only on 4th instar larvae.

Around the roots at the base of the oak saplings were chambers that extended to 7.5 cm below the soil line along the taproot and laterally around the roots up to 10 cm away from the taproot. There was a 1–3 cm space around the roots and a small amount of debris covering the opening at the soil surface. Trenches and tunnels (beneath a loose layer of dried grass and leaves), led away from the chambers to ant nests that were 1–13 m away. No 1st and 2nd instar larvae of *S. edwardsii* or membracid nymphs were found in the chambers with the ants during late April or early May.

By late May the ants had constructed conical structures (byres) of fine pieces of detritus (much like the material covering the ant nests) at the bases of the oak saplings (Figs. 1 & 2). The byres were 10 to 25 cm in dia. and extended 5 to 20 cm upward on the stems of the oaks. The largest byres were around the largest saplings (10.0 and 20.0 cm dia.). There was a 1.0–1.5 cm space between the inner side of the byre and the bark of the sapling confluent with the chambers around the roots (Fig. 2). The upper edge of the byre was contiguous with the bark of the sapling except for a series of 1–4 mm gaps which allowed access of the ants into and out of the byres.

The behavior of the larvae of *S. edwardsii* changed when they reached the 3rd instar (during late May). Although there was considerable evidence of feeding, larvae were not found on the foliage during the day. Instead, the mottled, brownish 3rd and 4th instar larvae remained during the day on the bark in the chambers within the byres at the base of the oak saplings. Only 4 larvae were found outside the byres during the day, and these were on branches of the 10 cm dia. sapling among aggregations of *S. camelus* nymphs and adults. The larvae in the byres were positioned vertically on the stem, at or above

FIG. 1. (**Top**) A 2.5 cm dia. *Q. velutina* with a byre (arrow) at base. (**Bottom**) Six 4th instar larvae of *S. edwardsii* with attending ants and a *S. camelus* nymph (arrow) within a byre at the base of a 1.9 cm dia. *Q. velutina*. The stem of the oak was pulled away from the observer to reveal the larvae in the byre. The membracid nymph is positioned where the upper edge of the byre had been.

FIG. 2.   A 3.5 cm dia. *Q. velutina* with a byre at base. A portion of the byre was removed to reveal the larvae and space (arrow) between inner side of byre and bark of sapling.

the soil line (Fig. 1). Between 1 and 114 larvae were found in the byres and the largest larval aggregations were in those byres on saplings with base diameters of 3.8 to 10.0 cm (Table 1). Larvae and byres were not found on *Q. velutina* and *Q. coccinea* with base diameters greater than 20 cm or on other species of shrubs or trees. Between 20 and 100 (an exact count was difficult) ants were in the chambers with the larvae in each of the byres. Only 3 *S. camelus* were found in the byres, although many nymphs and adults (and attending ants) were on the branches of the saplings. One 1.3 cm dia. sapling had 138 *S. camelus* nymphs and adults and 75–100 ants on it. The ants appeared to obtain honeydew from the membracids.

TABLE 1. Number of *S. edwardsii* larvae in byres at bases of *Q. velutina* and *Q. coccinea* saplings at locality 1. Observations were made on 8 June 1980 and 6 June 1981.

Sapling size (dia. at base in cm)	x̄ no. larvae[1] 1980	x̄ no. larvae[1] 1981
1.3	1.0 (2)	4.5 (2)
1.9	8.5 (2)	—
2.5	2.3 (3)	1.0 (1)
3.1	—	9.0 (1)
3.8	2.7 (3)	—
5.0	19.7 (3)	20.5 (2)
6.3	13.0 (1)	22.0 (1)
10.0	60.0 (1)	23.0 (1)[2]
20.0	3.0 (1)	—
>20.0	0.0 (8)	—

[1] Numbers in ( ) are the number of saplings examined in size class.
[2] Ninety-one larvae (out of 114) were removed from this sapling on 31 May.

The 3rd and 4th instar larvae of *S. edwardsii* fed on the foliage of the host only at night. They left the byres within one hour after sunset, crawled up the stem and fed on the foliage until sunrise, and then returned to the byre. On 14 June (1980), 4th instar larvae on a sapling (10 cm dia.) and a sucker clump (17 larvae in byre) were observed. A dim flashlight was used to observe the insects at night. Sunset on 14 June was 2117 h EDT and sunrise on 15 June was 0559 h. At 2140 h (0.5 h after sunset) one larva left the byre on the 10 cm dia. sapling. By 2155 h several more larvae had left the byre and were crawling up the trunk. One larva crawled at a rate of 1.3 cm/min. At 2225 h all 17 larvae on the sucker clump were crawling up the stems. Each larva was accompanied by 1–8 ants as it crawled up the stem. At least one ant was always within 2.5 cm of each larva, and occasionally an ant was observed on the dorsal surface of a larva. By 2300 h the larvae had begun to feed on the oak foliage and continued to feed throughout the night. Between 0605 and 0630 h (5–30 min after sunrise) the larvae began leaving the foliage and crawled down the branches and stems of the host. At 0615 h only 3 of the 17 larvae on the sucker clump were feeding, the rest had either entered the byres or were crawling down the stems. On the 10 cm dia. oak 2 larvae were crawling down the main trunk 2 and 3 m above the forest floor, while another larva was just entering the byre at the base of the oak. During this time the sky was overcast and the temperature was 21°C. No larvae were observed outside the byres after 0700 h. Throughout our observations ants were always on or within 2.5 cm of each larva and appeared to obtain honeydew from them.

On 31 May (1981), 91 larvae (out of 114) were removed from the 10 cm dia. *Q. velutina* for determination of parasitism. The larvae

were reared to maturity on fresh *Q. velutina* leaves. Percent parasitism was 26% and was due to Tachinidae and Braconidae. It is not known which larval stadia are attacked or the mode of parasitoid attack.

Pupation. Pupation occurred during late June and early July at the base of the host plant, either on the underside of leaves that were underneath or adjacent to the byre, or on the stem of the host within the byre. On 29 June, of the 17 larvae observed on 14 June, 6 had pupated on the underside of leaves adjacent to or under the byre, 3 were on the main stems in the byre (these were parasitized by braconid wasps), and 3 groups of braconid cocoons were on the underside of the leaves. This accounted for 12 of the 17 observed earlier.

The pupae of *S. edwardsii*, like many other lycaenids (Downey, 1966), produced a faint rattling or creaking sound. The sound was produced only after the pupae were disturbed. Because few ants were present in the byres (1–4) or on the saplings (less than 20) it remains unclear what role (if any) the sounds might play in the myrmecophilous relationship of *S. edwardsii* and *F. integra*. No *S. camelus* nymphs or adults were present, even though adults were abundant on 14 June. This might partially account for the paucity of ants on the saplings.

Adult behavior. One freshly emerged *S. edwardsii* adult was observed on 29 June (1981) and by 9 July adults of both sexes were numerous. Visual count suggested that between 250 and 350 individuals were within the clearing. Adults nectared on *C. americanus* and *R. hirta*. *C. americanus* was the dominent flowering plant at this time and was the major nectar source for the adults. *Harkenclenus titus* (Fabricius), *S. liparops* (Leconte), and *S. calanus* (Hübner) were also nectaring at the *C. americanus* flowers. Males of *S. edwardsii* were usually on leaves at the tops of the larger saplings and shrubs within and bordering the clearing. They frequently engaged in aerial "combat" with other hairstreaks that flew near them. The ants did not display any aggressive behavior towards the adult butterflies. An ant that encountered a female walking on a branch, stopped, palpated her with its antennae, and then walked away.

Oviposition of 2 *S. edwardsii* females was observed between 1330 and 1347 h on 9 July (1981). One female walked along a horizontal branch of a *Q. velutina* sapling, probed her abdomen into a knobby wound in a small fork, deposited an egg, and then flew away. The other female oviposited an egg in a vertical wound about 20 cm above the forest floor on a 3.1 cm dia. sapling. The egg was placed under the rough bark that formed the edge of the wound. During September, several *Q. velutina* saplings were examined for ova. All ova were either in old wounds or hidden under loose bark or dead wood, and occa-

sionally, empty egg shells from the previous year were adjacent to the newly laid eggs. In one wound 4 ova were stacked on top of each other. Most ova were between 0.6 and 1.5 m above the forest floor.

DISCUSSION

S. edwardsii is myrmecophilous as are many North American Lycaenidae. However, *S. edwardsii* departs from its congeners and other Lycaenidae in North America in that the 3rd and 4th instar larvae aggregate during the day at the base of the host within conical structures of detritus constructed by the ant, *F. integra*. The 3rd and 4th instar larvae feed nocturnally on the foliage and are frequently surrounded by a retinue of ants. Other *Satyrium* species are tended by ants, but they do not form aggregations and usually remain on the host leaves or fruit, leaving them only to pupate.

Fourth instar larvae of *S. edwardsii* produce honeydew on which ants feed. The larval aggregations might, therefore, provide a valuable, highly attractive and easily defended food resource for the ants as in many Australian and South African Lycaenidae (Clark & Dickson, 1971; Common & Waterhouse, 1972; Pierce & Mead, 1981). The byres should facilitate protection of larvae by ants and provide the ants with more ameliorating environmental conditions (higher relative humidity). The larvae in turn would gain protection from predator and parasitoid attack. In the riodinid, *Anatole rossi* Clench, "pens" were constructed by ants at the base of the host plant in response to the presence of a larva on the host but only after the honey glands became functional (Ross, 1966). However, it is unclear from the present evidence if the aggregations of *S. edwardsii* larvae provide the stimuli that induce byre construction by *F. integra*. The 3rd instar larvae of *S. edwardsii* which do not have functional Newcomer's organs also rest in the byres.

The membracid, *S. camelus*, and other homopterans associated with *S. edwardsii* larvae may play a role in the symbiotic relationship between *S. edwardsii* and *F. integra*. Membracids release honeydew and thus, become an important energy resource for the ants. The ants in turn become a resource for the membracids because they reduce predation on nymphs (Wood, 1977, 1982b). The effectiveness of ants in promoting membracid survival depends on factors such as the number of nymphs present, the proximity and size of the ant colony, and the longevity of the host plant (McEvoy, 1979; Wood, 1982a, b). Long-lived perennials like *Q. velutina* and *Q. coccinea* provide relatively predictable oviposition sites for female membracids. The nymphal aggregations that result provide a predictable energy resource for the ants. Ant colonies established close to such membracid host plants will

promote nymphal survival, as well as increased fitness to the ant colony (Wood, 1982a). The presence of nymphal aggregations of *S. camelus* near *S. edwardsii* larvae may concomitantly benefit the larvae by increasing the number of ants in their vicinity. This may be particularly important for the protection of early instar larvae which are incapable of producing an energy resource (honeydew) for the ants. Compounds produced by the epidermal glands probably facilitate protection of the early instar larvae by keeping those ants already present in their vicinity.

The pupae of *S. edwardsii* produce a faint creaking or rattling sound after being disturbed. Downey (1966) reported sound production in pupae of six additional *Satyrium* species, as well as in many other lycaenids and three riodinids. The stridulatory organs are located between the fifth and sixth abdominal tergites and produce the noise when the abdominal segments are rapidly moved. It is not clear what the function of the sounds is for *S. edwardsii* or other Lycaenidae (Downey, 1966). In *A. rossi* the stridulatory organs in conjunction with pupal glands on the metathoracic segment appear to serve as ant-attractant organs (Ross, 1964, 1966).

The myrmecophilous relationship between *S. edwardsii* and *F. integra* is undoubtedly one of the more advanced symbioses known among any of the North American Lycaenidae and ants. Additional studies are required to ascertain the degree of protection of the larvae offered by the ants from predation and parasitism and to detail the precise relationships between *S. camelus, S. edwardsii*, and *F. integra*.

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